CHANGES IN THE STATUS OF THE RED WOOD ANT FORMICA RUFA L. (HYMENOPTERA: FORMICIDAE) IN NORTH WEST ENGLAND DURING THE 20TH CENTURY

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Abstract. The red wood ant Formica rufa L. has declined in the Lake District during the course of the century, and has virtually disappeared since the 1950s. However, there are still thriving populations on limestone sites in both the Lancashire and Cumbria parts of the Arnside–Silverdale Area of Outstanding Natural Beauty (AONB), where it is present at 8 locations. The north end of Underlaid Wood, at SD492798, is now the northern limit of the species' range in England. Factors contributing to the decline are discussed, with the conclusion that the most likely cause of the collapse of the Lake District populations was a 3 year run of abnormally heavy May rainfall in 1966–1968, which caused extinction on several sites, after which the surviving populations continued to decline. The status of the remaining populations in the AONB, which do not appear to be under threat and are mostly on sites receiving favourable management, is reviewed.

BACKGROUND TO THE SURVEY

The wood ants Formica rufa L. and Formica lugubris Zetterstedt construct conspicuous mound nests, usually in woodland. Satchell & Collingwood (1955) reported the results of surveys in 1954 in the English Lake District. F. rufa was found in abundance in the South Lake District near Arnside and Grange-over-Sands, sparsely around Windermere (lake, not town) and at three isolated sites further north. F. lugubris was found to be present in the woodlands of the Duddon Valley from Duddon Bridge up to Seathwaite, and in Borrowdale around Ashness Bridge and up the Lodore Beck. The distribution of F. lugubris has not changed in the past 45 years. It is still common in the woodlands of the Duddon Valley (Karen Sampson, English Nature, pers. comm., and N.A.R. obs. 1998). In Borrowdale its nests can readily be seen beside the Ashness Bridge car park and along the roadside through Lodore Woods. However, a preview of the distribution map for F. rufa (Edwards, 1997) indicated that it had disappeared from its former locations in the Lake District. though it was still present in the Arnside area. Decline of F. rufa populations has also been reported in Wales (Fowles, 1994), and in Cheshire, where they have disappeared from the Delamere Forest (Carl Clee, pers. comm.). It was to investigate the current distribution of F. rufa in Cumbria and Lancashire, and the possible reasons for its decline, that this study was begun in 1996, and completed in 1999 with support from English Nature's Species Recovery Programme, with some final updating in 2000. This account draws heavily on the 1955 paper for historical details.

CHANGES IN DISTRIBUTION BEFORE 1954

Satchell & Collingwood (1955) described *F. rufa* as being found in abundance on Carboniferous limestone near Arnside and Grange-over-Sands, and sparsely on the Silurian slates and flags around Windermere. There were, in addition, three isolated sites: at Hoff Lunn near Appleby, Parson's Park, Caldbeck, each with a few colonies only, and Dodd Wood on the Bassenthwaite slopes of Skiddaw, representing the

most northerly outposts of the species. They distinguished between sites on the Carboniferous limestone along the southern edge of the Lake District and around Arnside (now known as the Morecambe Bay Limestone Natural Area) and those on the Silurian slates and flags and other formations further north (Lake District Fells and Dales Natural Area). They concluded that, in the latter, wood ants were already in decline because, although there were still 7 active sites on these rocks (Table 2, Section A), there were also 9 sites where colonies had become extinct during previous decades (Table 1).

The locations of both categories of these sites are shown by tetrads in Fig. 1 (not all the sites appear because in some cases more than one occur in a single tetrad). The 1955 authors did not give grid references, but the sites have been located to the nearest 1 km square of the national grid from their table of sites (which also gives details of geology and woodland type). The 1 km square references are given in the Tables 1 and 2. Some which could not be located accurately are indicated by "?".

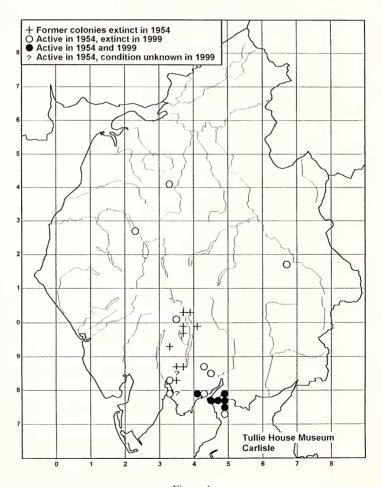


Figure 1

Table 1. Former sites extinct by 1954

SD3787	Ants used to be carried to Graythwaite for pheasant food
SD3797?	•
NY3802	Recorded 1912
SD3392?	One colony last seen about 1924
SD3483?	Ants last seen about 1929
SD3799?	Ants last seen about 1934
SD4098	Ants last seen about 1934
SD3587	One colony last seen about 1939
NY3602	Ants last seen about 1947
	SD3797? NY3802 SD3392? SD3483? SD3799? SD4098 SD3587

Table 2. Sites with colonies in 1954

Site	Grid ref.	Nests in 1954	Condition by 1999
Section A: Sites on a	cid rock		
Hoff Lunn Dodd Wood Parson's Park Burn Barrow Wood Haverth. Heights Ellerside Breast Roudsea Wood	NY6616 NY2327 NY3340 SD3482 SD3484 SD3579 SD3282	1 nest numerous but localised several nests several nests 1 nest 3 nests 1 nest known 1960s	last seen 1967 absent 1993 absent 1993 not checked not checked not checked active until 1996, defunct 1999
Section B: Sites on li	mestone		
Part 1: north side of		•	
Blawith Fell Eggerslack Yew Barrow Meathop Fell High Crag Wood Park Wood White Scar Old Park Wood	SD4178 SD4078 SD4078 SD4379 SD4485 SD4386 SD4585 SD3378	numerous numerous 1 nest numerous numerous numerous 1 nest numerous, 30 counted	3 nests in 1996, 2 nests by 2000 2 nests in 1996, expired 1998 not found 1996 several nests 1988, absent 1999 absent early 1970s, ditto 1996 absent early 1970s, ditto 1993 not checked absent 1993
Part 2: Arnside-Silve	rdale area		
Cumbria Arnside Park/Knott	SD4477	numerous	numerous, larger area, at least 100 nests
Underlaid Wood Marble Quarry Major Woods Grubbins Wood	SD4878 SD4978 SD4978 SD4478	numerous not known not known not known	widely distributed, est. c. 90 nests 7 nests found in 1999 20 nests found in 1999 13 active nests in 1999
Lancashire Gait Barrows Cringlebarrow Eaves Wood Grisedale Wood Trough Plantation	SD4877 SD4974 SD4677 SD4873 SD4875	numerous numerous numerous but localised numerous numerous but localised	abundant, over 100 nests counted 1996 present, 20 nests counted 34 nests counted in 1999, scattered absent absent

Of the 22 sites where *F. rufa* was found, 15 were in the Arnside-Grange area, extending from Old Park Wood in the west, through the Grange area, to Whitbarrow in the east; and from Arnside south to Cringlebarrow. These are shown in Fig. 1 and listed in Table 2, Section B (which also gives their condition at the end of the present survey). The 1955 paper discussed physical factors possibly influencing distribution. It was concluded that the rather open limestone woodlands of the South Lake District, free draining and with a high proportion of bare, well insolated rock, provided more suitable conditions for *F. rufa* than woods on other formations in the area. It was also noted that this area, besides its limestone geology, differed climatically from the Windermere area. The 49°F (9.4°C) isotherm (average mean of the daily mean temperatures 1901–30) corresponded roughly with the northern limit of the area in which *F. rufa* was abundant, and the average annual rainfall of Arnside was about 22 inches (56 cm) less than that of Windermere.

Changes between 1954 and 2000

By the end of the recent survey it was concluded that all the colonies on the northern acid rocks had expired, and that only 2 nests survived on limestone (at Brown Robin) on the north side of the Bay. There was, however, no indication of decline in the Arnside–Silverdale AONB.

In the early 1970s people began to notice that wood ants had disappeared from most of the sites on limestone in the South Lake District where they had previously been numerous, though now, so long after the event, it is not easy to establish the facts. During this period Peter Howard (pers. comm.), then at Merlewood Research Station, noticed grassed-over mounds in Eggerslack Wood, which probably were defunct F. rufa nests (though on this site 2 nests did survive until 1998). It seems that in the same period the ants had disappeared from their stronghold in Old Park Wood, Holker, where 30 nests had been counted in 1954, and from Witherslack Woods where there had been numerous nests on the woodland edge along the foot of the scree below Whitbarrow, and local people had noticed their absence in the early 1970s (Cedric Collingwood, pers. comm.). In Limegarth Wood on Meathop Fell, where there had been numerous nests in 1954, Cedric Collingwood noticed a decline in 1967–69. From these observations, and the general recollections of local people canvassed by Cedric Collingwood, it appears that a drastic decline of F. rufa on South Lake District limestone sites took place in the last few years of the 1960s, to the extent of extinction on some of the sites by the early 1970s.

The only limestone sites on the north side of the Bay where wood ants are known to have survived are: Meathop (Limegarth) Wood where several nests were still present in 1988 (Michael Sykes, ex-ITE, pers. comm.), Eggerslack Wood with 2 nests until 1998 and Brown Robin (Blawith Fell) with 3 nests in 1996, but only 2 by 2000. Checks by Cedric Collingwood in 1991–93 at Old Park Wood and Witherslack found no wood ants. However, there is no indication of decline in the wood ant population on Arnside Knott, only 2 km in latitude further south, and wood ants were abundant on Gait Barrows, in Lancashire, when the NNR was established in 1975.

Little information is available about the fate of the outlying northern colonies during this period. The Hoff Lunn nest was last recorded in 1967, when a note initialled P.S. in the *Field Naturalist*, Vol. 11 No. 4, 1967, reported that: "a very small nest was found in birch scrub this summer some 80 yards from the original site". In

1991–93 Cedric Collingwood found that they were no longer present at Dodd Wood, Skiddaw, or at Parson's Park, Caldbeck.

No attempt was made during the survey to trace the nests known in 1954 at Ellerside Breast, Burn Barrow Wood or Haverthwaite Heights because there was no precise location information and too large an area to search. There had only been a few nests, even in 1954. Renny Park Coppice was visited in 1999 but no nests were seen in this acid oak woodland, which contained much rhododendron and clearly had been managed as a pheasantry in the past. The Dodd Wood and Calbeck sites had been reported as defunct by Cedric Collingwood by 1993. Stephen Hewitt was unable to find the Hoff Lunn nest in 1999, but there was no information about its former location on this large site. In 1998 I learned that there had been a single nest at Roudsea Wood (SD3282), situated in a conifer plantation on Silurian rock. This nest had been known to Cedric Collingwood, though not during the original survey, but is presumed to have been present at that time. It was known to the NNR staff into the 1990s, but was found to be defunct in 1999.

CHANGES WITHIN THE SURVEY PERIOD 1996–2000

A request for current records of *F. rufa* was published in the *Carlisle Naturalist* in March 1996 (Vol. 4, No. 1). The only positive information which was received was that they were still present at Brown Robin (SD4178), the Cumbria Wildlife Trust (CWT) Reserve on Blawith Fell near Grange-over-Sands. In 1996 three nests were found in a coppice exclosure: one very large, clearly long-established, and 2 smaller colonies. Two long-established nests were also found in nearby Eggerslack Wood (SD4078). In March 1997 they were beginning to be active, but May was a very wet month (Table 3) and in the autumn they were all found to have accumulated very little thatch, suggesting they had not had a good season. In 1998 it was found that both nests in Eggerslack Wood had expired, as had also the largest one in Brown

Table 3. Monthly rainfall at Merlewood (mm)

	April	May	June
1959	121.0	42.5	116.2
1960	92.6	79.1	73.0
1961	144.8	50.6	72.2
1962	99.3	91.8	62.8
1963	93.7	84.5	92.1
1964	74.3	99.9	101.2
1965	77.5	84.7	124.4
1966	92.0	122.7	139.8
1967	39.5	133.4	68.7
1968	61.5	104.2	92.4
1969	79.6	93.8	89.7
1970	142.1	27.6	57.2
1996	88.2	63.2	38.0
1997	33.9	115.7	72.8
1998	64.2	47.5	175.1
Mean	72.0	70.5	82.0

Robin. A check of nests on Arnside Knott and Gait Barrows found no corresponding decline in these sites further south. By October 1999 the larger of the two survivors in Brown Robin seemed to be defunct, having disappeared, like all the surrounding area, under dense growth of bramble, but in 2000 was found to be still active. The other colony had moved from its mound to a more favourable site. It looked very weak, but was still surviving in 2000.

Possible factors responsible for decline, before 1954

At the time of the 1954 survey the populations of F. rufa on the limestone appeared to be stable, but those on the Silurian rock further north were clearly in decline. The more stringent climatic conditions in the Windermere woodlands and the reduction of ground insolation by invading bracken were considered by the 1955 authors to be the major factors contributing to the decline. However, they had found records, and much anecdotal information, which suggested that many of the locations on the Silurian had been introductions. The practice of introducing wood ants into pheasantries was widespread towards the end of the 19th century; attempts being made to establish colonies as sources of brood for feeding to young pheasants. The colonies at Renny Park Coppice, Beck Pane Wood and other parts of the Brathay Hall Estate had been introduced, according to local information, about 60 years earlier. The ants at Haverthwaite Heights were also said to have been introduced, likewise those at Dodd Wood, near Keswick, and there had been an unsuccessful attempt to establish them on the Lowther Estate near Penrith from Hoff Lunn. There was also supposed to have been an unsuccessful attempt to introduce ants from the Duddon to the Grizedale Estate—the only report of an introduction involving F. lugubris. This activity must have involved removing colonies from their habitat and depositing them in sites not of their choosing, and, more seriously, outside what seems to have been their natural northern climatic limit at the time. It is, therefore, not surprising that they did not thrive. It seems significant that only at Dodd Wood were nests described as numerous, elsewhere usually one or a few, suggesting that this was the only site where introduction had succeeded in establishing a population. The fact that they persisted so long at other places, before finally expiring, suggests remarkable vigour and tenacity on the part of the species.

It was, however, interesting to observe during the survey that wood ants can coexist with pheasant rearing. Pheasants may scratch and scatter nests but do not seem to do serious damage to the colonies, unlike badgers, which sometimes deeply excavate them. Sometimes nests were found next to pheasantries, in clearings made for the birds. Green woodpeckers, which certainly eat ants, have been suspected of damaging colonies, making conical holes in the mound, particularly in autumn, and leaving characteristic "cigarette-end" droppings, but this damage seems to be only superficial.

Possible factors after 1954

Loss or mismanagement of habitat is frequently blamed for loss of species, but a surprising feature of the drastic decline of *F. rufa* on South Lakeland limestone sites in the late 1960s is that the ants disappeared from sites where the habitat had not changed and still appears to be suitable. At Old Park Wood, for instance, there is bare limestone in patchy woodland, and along the foot of Whitbarrow there is still, along the woodland edge, well insolated scree sheltered by overhanging cliffs, exactly

as described in 1955. This, and the fact that the ants disappeared or declined over such a wide range of sites at the same time, while apparently being unaffected only 2 km in latitude further south, suggests that a climatic factor was the primary cause of the collapse of the south Lakeland populations.

The best-remembered event of this period was the exceptionally severe winter of 1963, when the ground was frozen to unprecedented depths. This, however, is unlikely to have been responsible since *F. rufa* is unaffected by the prolonged subzero conditions of Scandinavian winters (Cedric Collingwood, *pers. comm.*). The effects of heavy rainfall at critical times in the life cycle seem a more probable cause. In Cedric Collingwood's opinion (pers. comm.), the critical period is May, when the colony is rearing the new season's brood. If this is successful the colony can survive even a bad summer. Conversely, failure to rear the brood may render the colony unable to carry out its functions; and hence to survive. Merlewood Research Station, near Grange-over-Sands, began recording minimum and maximum temperature in 1980, but has been keeping rainfall records since 1959. These show that May, on long-term average, is the driest month of the year, which must generally be favourable to the ants. However, Table 3 gives the monthly rainfall (mm.) for April, May and June 1959–1970, and also for 1996–1999, as the latter appears relevant to recent events. This shows that May 1966, 1967 and 1968 had exceptionally high rainfall, being 74%, 89% and 48% in excess of the long-term mean for the month. The wet May of 1966 was also followed by an exceptionally wet June: 70% over the mean. Rainfall in May of over 100 mm has occurred sporadically in other years, but 1966–1968 are the only three years in the recording period in which it occurred in succession. The present author considers this run of consecutive wet springs to be the most likely cause of the collapse of F. rufa populations at that time. The wet May of 1997 is also suspected of contributing to the demise of the 2 nests in Eggerslack Wood and one in Brown Robin, and probably also the one at Roudsea.

This conclusion raises questions as to why the populations in the Arnside area, only 2 km in latitude further south, were not affected; and why those populations which survived the 1966–1968 collapse did not recover. No information is available as to how the Arnside populations fared in the 1960s, but, as only two populations have disappeared and the remainder appear vigorous, it can be concluded that they were not seriously affected. No comparable monthly rainfall figures have been obtained, but the meteorological information of the 1955 authors indicates an annual rainfall of about 1016 mm for Arnside, whereas the long-term monthly mean for Merlewood gives 1212 mm. This suggests that the rainfall at Arnside could have been less in the critical period. Small differences in climatic conditions can have a disproportionately large effect on species at the edge of their range, and it appears that the events of 1966–1968 initiated a contraction of the northern limit of *F. rufa* in North West England by 2 km of latitude. By circumstances of geography, this was enough to render it almost extinct in the southern Lake District. The three places where it survived longest are clustered around Grange-over-Sands, which is noted for its mild climate.

The question as to why the surviving populations did not recover requires (brief) consideration of the biology and the habitat requirements of the species. Males and queens emerge from nests in June and mating takes place on or near the nests, after which the queens shed their wings. Although literature states that mated queens can establish nests by taking over colonies of *F. fusca* or *F. lemani* (Skinner & Allen, 1996), this seems to have rarely been observed. It is probable that colonies most commonly propagate through budding, in which mated queens return to the natal nest and recruit a group of workers to move out and establish a new colony. With

regard to habitat, F. rufa is a shade-tolerant woodland ant which maintains higher than ambient temperature in the nest in summer using metabolic heat derived from their intake of carbohydrates in 'honeydew' from aphids (Bryan, 1977; Pontin, 1996). Measurements of the percentage of the potential insolation which was actually reaching ant nests in the south of England (Pontin, op. cit.) indicated that F. rufa nests were most commonly found in partial shade, but could persist in under 25% insolation, and fewest were found in over 75%. General observations suggest that the picture is much the same in the North West of England. Nests are commonly found in sheltered situations receiving some sunlight, e.g. on woodland edges, or by the sides of rides and paths, often just under the edge of the branches of an adjacent tree or shrub. However, on Arnside Knott a few, usually with very low mounds, are on totally exposed slopes and some, usually very large old nests, can be found under closed canopy, and the latter was observed on several other sites. Indeed. observations by the author during the survey period suggested that F. rufa populations can exist in two contrasting modes, which might be termed the "dynamic" and the "static". The dynamic state is found on sites with good diversity of conditions, such as Arnside Knott and Gait Barrows NNR, where one frequently finds new nests, composed only of thatch, "middle-aged" nests which are developing soil bases and very old nests with soil bases 3 m or more in diameter, often becoming shaded and abandoned. There is clearly a continual turnover of nests as colonies move or expand. The static state is seen on sites with closed canopy, such as Major Woods and parts of Cringlebarrow-Deepdale. Here there are few, if any, new nests but widely separated very large old nests, typically with tall steep-sided conical mounds on very wide soil bases. The availability of good forage trees from which the workers can obtain honeydew and insect prey is likely to be the critical factor in enabling these shaded colonies to persist, but it is not certain that they can survive indefinitely under these conditions. The environment of nests must therefore be profoundly affected by woodland management. The practice of coppicing (cutting woods on rotation and promoting regrowth from stumps) which would have maintained the ant's most favoured habitat, was the main mode of woodland management in the Lake District from the Middle ages to the 1914-1918 War. In the Midlands F. rufa can live under closed canopy (Cedric Collingwood, pers. comm.) but under the more stringent climatic conditions of the southern Lake District the decline of coppicing and consequent exclusion of sunlight by closure of the canopy is likely to have been generally disadvantageous to the ants. This situation can be seen in the sites where F. rufa persisted for a time. Limegarth Wood (Meathop Fell) was last coppied in 1940 (Michael Sykes, per. comm.) and has gradually reverted to closed canopy. Eggerslack Wood has not been actively managed recently, and coppicing was not resumed in Brown Robin until 1995.

A further factor militating against the survival of small populations is likely to be decline in vigour due to reduction of the gene pool. Mating of queens outside the nest with males from other colonies gives the potential for reinvigorating the stock by outbreeding, but this must decrease as the number of nests decreases. This probably explains why one or two nests may persist on a site for a very long time, but

gradually become weaker.

STATUS OF POPULATIONS IN 2000

In the Arnside-Silverdale AONB the more open conditions of some of the sites, their management as woodland resource or for rare butterflies by coppicing, glade creation and scrub control, and the more favourable climate can account for the

ant's continued presence. At present the populations appear to be stable and not under threat. The 1954 locations were confirmed, except for Trough Plantation where no nests were found, and Grisedale Wood where the owner and keeper both assert that there are no wood ants. However, 3 sites were found which did not figure in the earlier survey, giving a total of 8 locations.

Attempts were made to count the nests on all the extant sites, in order to put minimum sizes on the populations, but this proved impractical for large sites, for which estimates had to be based on partial counts. The results are summarised in Table 2. Section B, and the sites can be classed as follows:

Major Populations

Gait Barrows NNR (Lancs.)—112 nests counted by students in 1996 (Farinacci & Smith, 1996).

Arnside Knott SSSI (Cumbria)—encompasses the hill of the Knott and Heathwaite (National Trust) and the private woodlands of Copridding and Arnside Park. The 1955 report named and mapped only Arnside Park, which is now dense woodland, but the population is much more extensive. In 1999 National Trust staff counted 70 nests on the Knott. As c.20 can be seen along the cliff-top path on the south of Arnside Point, and they are also present in Frith Wood and on Heathwaite, the total population of the SSSI must be at least 100 nests.

Underlaid Wood SSSI (Cumbria)—30 nests were counted in the part south of the footpath to Fairy Steps. As this is about one-third of the SSSI, and similar habitat with nests extends to the north end, an estimate of c.90 nests can be made. The north end is now the northern limit of range of *F. rufa* in England as it is about 9 km north in latitude of the only remaining colony in Yorkshire, at Dallowgill (SE1871).

Medium populations

Cringlebarrow-Deepdale SSSI (Lancs.)—20 nests counted in Deepdale and extending onto the south end of Cringlebarrow.

Eaves Wood SSSI (Lancs.)—National Trust staff counted 34 nests in 1999.

Major Woods (Cumbria)—20 nests counted, probably more.

Minor populations

Marble Quarry and Hale Fell SSSI (Cumbria)—only 7 nests found, though more have been reported (Martin Colledge FC, *pers.comm.*), but it only seems to support a small population.

Grubbins Wood CWT Reserve (Cumbria)—10 large active nests found, and 3 small ones.

Brown Robin CWT Reserve (Cumbria)—2 nests, one very weak.

IMPLICATIONS AND GUIDELINES FOR CONSERVATION MANAGEMENT

Although nests can persist for a long time under closed canopy, they are most active in more diverse conditions.

Wood ants benefit most from continual low-key management operations which do not drastically alter the habitat: e.g. selective thinning or timber extraction, coppicing and the creation of glades for butterflies or pheasants.

Once woodland has become over-mature it is dificult to retrieve the situation, because heavy thinning or drastic coppicing may remove trees which shelter nests from rain, and important forage trees near nests, without necessarily reducing

shading by other trees. Alternatively, if it does admit light it may promote the growth of ground vegetation such as bramble which can smother nests and indeed the whole woodland floor.

Because of their dependence on colony reproduction by budding, if conditions become unfavourable they are unable to respond by dispersing into new sites. Therefore they need to be conserved where they are.

Although, as a generalisation, any low-key management is better than than none at all, wherever possible woodland management should take account of the needs of individual wood ant nests. Trees or shrubs which shelter nests, usually on the north. should not be removed, but it is beneficial to admit more light from the south and west and to create open areas nearby into which new colonies can establish.

THE "GUEST ANT" FORMICOXENUS NITIDULUS (NYLANDER).

This tiny (3 mm) ant lives only in nests of F. rufa and related species of wood ants, apparently stealing food from its hosts, but not harming them or being harmed by them. It is rarely seen except in autumn when males, which are wingless and resemble workers, emerge onto the surface of the mound. During the survey they were seen on nests on Gait Barrows NNR and Arnside Knott SSSI (Robinson, 1998, 1999) and at Underlaid Wood SSSI. They were not seen at Eaves Wood SSSI, but have been reported there by Keith Alexander (NT) and Cedric Collingwood (pers. comms.)

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REFERENCES

Brian, M. V. 1997. Auts. The New Naturalist Series. Collins.

Edwards, R. (ed.) 1997. Provisional Atlas of the aculeate Hymenoptera of Britain and Ireland Part 1. Bees, Wasps and Ants Recording Society. Huntingdon: Biological Records Centre.

Farinacci, M. & Smith, C. 1996. Survey of the wood ant Formica rufa at Gait Barrows NNR.

Unpublished report to English Nature.

Fowles, A. P. 1994. A review of the ecology of the red wood ant Formica rufa L. (Hymenoptera, Formicidae) and its status in Wales. Conservation Ecology in Wales No. 1. Countryside Council for Wales.

Pontin, J. 1996. Ant Nests, Sun and Shade—their measurement and significance for invertebrate conservation. British Wildlife 8: 21-27.

Robinson, N. A. 1998. Observations on the "Guest Ant" Formicoxemus nitidulus (Nyl.) in nests of the Red Wood Ant Formica rufa L. in 1997. British Journal of Entomology and Natural History 11: 125-128.

Robinson, N. A. 1999. Observations on the "Guest Ant" Formicoxenus nitidulus Nylander in nests of the wood ants Formica rufa L. and Formica lugubris Zetterstedt in 1998. British Journal of Entomology and Natural History 12: 138–140.

Satchell, J. E. & Collingwood, C. A. 1955. The Wood Ants of the English Lake District. North West Naturalist, March 1955.

Skinner, G. J. & Allen G. W. 1996. Ants. Naturalists' Handbooks 24. Richmond.